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Possible causes of amphi-Atlantic distribution of *Orchestia gammarellus* (Pallas, 1776) (Crustacea, Amphipoda, Talitridae) in the North Atlantic: a review

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Abstract

Hypotheses concerning the modern distribution of *Orchestia gammarellus* (Crustacea, Amphipoda, Talitridae) and its causes in the North Atlantic are discussed. The synanthropic dispersal hypothesis of Henzler and Ingólfsson (2008) considers *O. gammarellus* as originating on the eastern shore of the North Atlantic and being transported by humans to Iceland and the western Atlantic shore (Newfoundland and the Maritime Provinces of Canada). The Eocene and natural dispersal hypothesis of Myers and Lowry (2020) proposes a geologically earlier origin of *O. gammarellus* when the west and east shores of the North Atlantic were still connected. Present day amphi-Atlantic distribution was explained by vicariance, with the vicariant event causing separation of *O. gammarellus* being continental drift drawing apart the west and east shores of the North Atlantic. A post-glacial natural dispersal hypothesis proposed herein, involves transport on ice floes or in driftwood from European shores to Iceland and the Atlantic Provinces of Canada. The small genetic distances amongst populations found by Henzler and Ingólfsson (2008) at the COI gene are inconsistent with the Eocene vicariance hypothesis. On evolutionary grounds, we question Myers and Lowry's (2020) designation of the Icelandic and Canadian populations as a new species of *Orchestia*. Existing molecular and morphological data are insufficient to distinguish between human-aided dispersal and natural rafting.

Key Words

evolution, dispersal, North Atlantic, *O. gammarellus*, zoogeography

Introduction

The talitrid amphipod *Orchestia gammarellus* (Pallas, 1766) occurs in the supralittoral of both north-eastern and north-western coasts of the Atlantic Ocean. It is one of only three North Atlantic talitrids, the other two being *Platorchestia platensis* (Krøyer, 1845) and *P. monodi* (Mateus, Mateus & Alfonso, 1986), which are amphi-Atlantic (Wildish and Chang 2017). The latter authors describe all three of the recognised amphi-Atlantic species as primarily being wrack generalist ecotypes.

In this presentation, the literature on *O. gammarellus* is reviewed as it pertains to its distribution and origins on both coasts of the North Atlantic Ocean.

Zoogeography

The known distribution of *O. gammarellus* within the North Atlantic Ocean is shown in Fig. 1. In the Mediterranean Sea, the most southerly records are from the North African coast at 35°N (Bellan-Santini and Ruffo 2003). In the northeast Atlantic, the most southerly records of *O. gammarellus* are on the island archipelagos (of Azores, Madeira, Canaries, Dahl (1967); Wildish (2012)) with the Canary Islands at 28°N being the furthest south. *Orchestia gammarellus* is present in the brackish waters of the Baltic Sea (Persson 1999). The most northerly records are from the Lofoten Islands in northern Norway (Stephensen 1940) at 68°N. This species is present in

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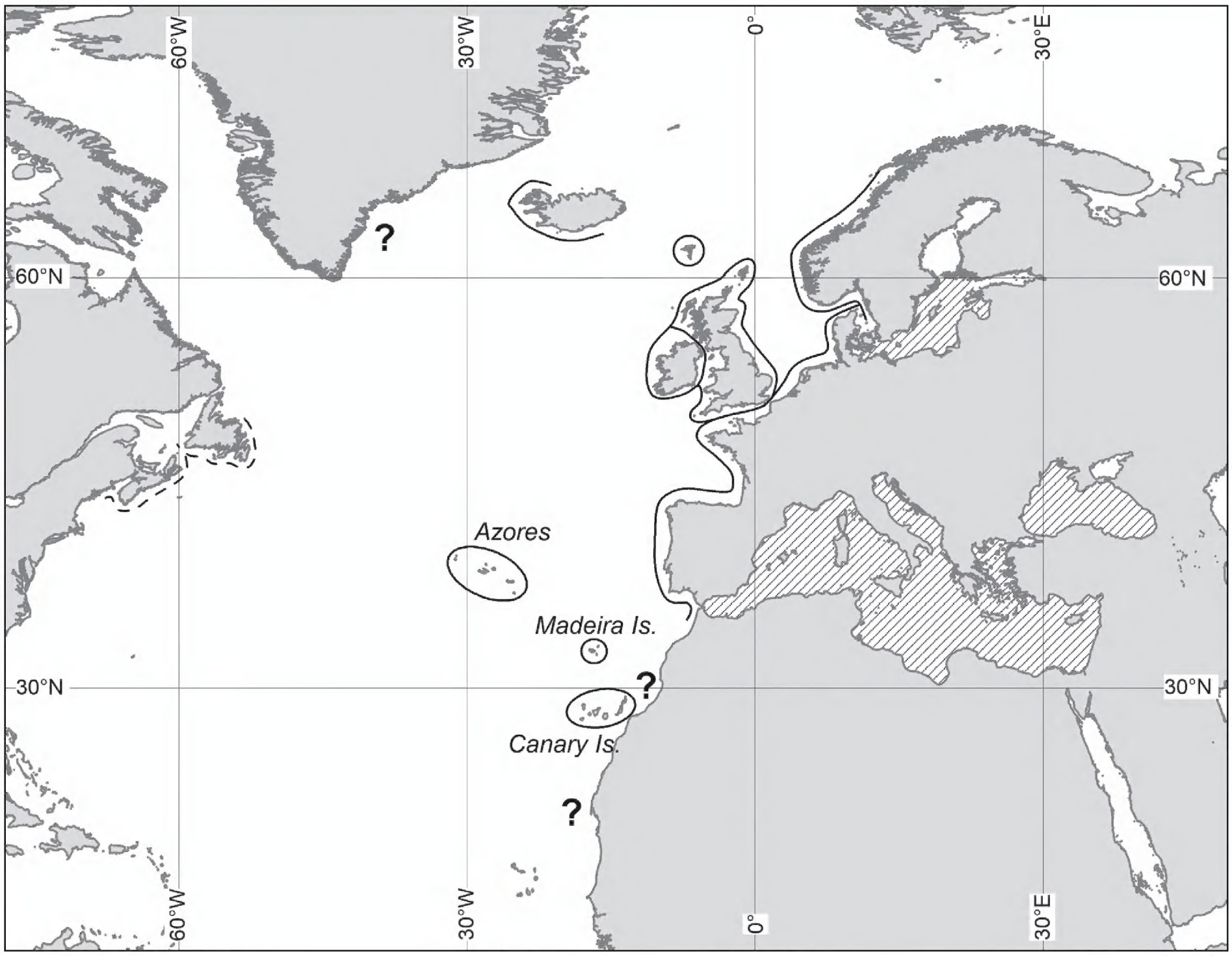

Figure 1. Map of the North Atlantic showing the distribution of *O. gammarellus*. Dashed line indicates intermittent presence on Canadian shores. Continuous line indicates presence (but not necessarily contiguous distribution) on Icelandic, European and Atlantic archipelago shores. Fill lines suggests presence at some coastal locations within each inland Sea. Question marks indicate that no published data of *O. gammarellus* distribution were found in this area.

southwest Iceland, where it was found for the first time by Ingólfsson (1973) in 1968. Sæmundsson (1937) thoroughly sampled intertidal amphipods and isopods in Iceland and did not collect *O. gammarellus*, which led Henzler and Ingólfsson (2008) to conclude that it was absent from southwest Iceland in the early part of the 20th century. The species has subsequently been found in north-western Iceland where local isolated populations are present near warm springs on or near a beach (Henzler and Ingólfsson 2008). The most easterly records are from the Black Sea (Bellan-Santini and Ruffo 2003). On the west coast of North America, *O. gammarellus* is present sporadically in Newfoundland, Nova Scotia and New Brunswick, the most southerly record being from Casco Bay (at ~ 44°N) in Maine (Bousfield 1973).

We note that only one species of true *Orchestia* Leach, 1814: *O. gammarellus* (= *O. forchuensis* Myers & Lowry, 2020) is present on the northwest Atlantic coast. On the north-eastern Atlantic/Mediterranean coasts, there are at least five species present: *O. gammarellus*, *O. mediterranea* A Costa, 1857, *O. aestuarensis* Wildish, 1987, *O. montagui* (Audouin, 1826) and *O. xylino* Lowry & Fanini, 2013. However, two independent molecular phylogenies (Pavesi et al. 2015; Davalos et al. 2018) both show that the current morphologically defined genus *Orchestia* is not monophyletic and that a future taxonomic revision is needed to correct this. Following such a revision, it is likely that only *montagui* (Audouin 1826) would be removed from *Orchestia* to a new genus. The concentration of four remaining species on the north-eastern Atlantic/Mediterranean coast is the *Orchestia* species hotspot and may represent its zoogeographic epicentre.

In summary, *O. gammarellus* is present on the eastern shore of the North Atlantic Ocean between the geographical bounds of 28 to 68°N, and on the western shore between 44 and 65°N.

Hypotheses explaining amphi-Atlantic distribution in the North Atlantic

Three hypotheses concerning the evolution of *O. gammarellus* in the North Atlantic Ocean have been proposed:

1. **Synanthropic dispersal.** *Orchestia gammarellus* reached Iceland, Newfoundland and the Maritimes of Canada in historic times following some form of synanthropic dispersal. The source population was thought to be from an unknown location on the north-eastern shore of the North Atlantic (Henzler and Ingólfsson 2008).
2. **Eocene natural dispersal.** In the Eocene (55,000,000 to 34,000,000 years BP), a 'proto-*gammarellus*' crossed the Scotland-Greenland land bridge by natural dispersal to reach Iceland and North America. The present-day distribution is represented by the survivors of this dispersal following further continental drift which isolated the North American, plus Icelandic, survivors from the eastern North Atlantic population (Myers and Lowry 2020).
3. **Post-glacial natural dispersal.** Natural dispersal via rafting during the post-glacial period carried *O. gammarellus* from Norway or Scotland to Iceland and Canada. Postglacial climatic and oceanographic reconstructions of this area at 18,000 years BP show a solid ice sheet extending to Iceland and with seasonal ice cover to the south of Iceland in the winter (Kellogg 1980). During a postglacial warming period at 10,000 years BP, the solid ice sheet was pushed to the north of Iceland, with ocean currents going westwards along the ice front towards Iceland (Buckland et al. 1986). The last author proposed that terrestrial insects (beetles and caddis flies) arrived in Iceland on ice floes transported from Norway, south of the ice sheet, in the westward current. Could it be that *O. gammarellus* used the same transport system: wrack on westward-flowing ice flows to get to Iceland? Another unexplored possibility is that dispersal from European shores was by driftwood-acclimated *O. gammarellus* carried in floating driftwood to Iceland and Atlantic Canada.

Evidence for/against the hypotheses

Morphology

A morphological analysis of 16 *O. gammarellus* populations from Canadian, Icelandic and European locations was conducted by Henzler and Ingólfsson (2008). For the non-sexually dimorphic characters chosen, all populations differed significantly in one or more characters. Including within larger geographic areas (e.g. Iceland), with evidence that warm spring populations within Iceland differed the most. This is evidence that environmental variations have influenced morphometry. Henzler and Ingólfsson (2008) consider that the morphometric results were consistent with a recent (in geological terms) post-glacial, European origin.

Myers and Lowry (2020) proposed a new name for the Canadian and Icelandic populations of *O. gammarellus*, based on four minor morphological differences. The distinguishing features of *O. forchuensis* from *O. gammarellus* (in brackets) listed by Myers and Lowry (2020) are:

- In adult male, p7 merus parallel-sided and 2× as broad proximally (versus merus triangular and 3× as broad proximally)
- In adult male, p7 carpus much longer than broad (versus almost as broad as long)
- In adult female, the basis of p7 is sub-ovoid (versus sub-quadrangular)
- In both sexes(?), p5 has a weakly developed posterodistal lobe (versus well-developed posterodistal lobe).

These characters apply to adults and cannot distinguish immatures and juvenile members of the two populations.

Morphological plasticity has been recognised within talitrids, notably those species living in a wrack primary ecotope, such as *Platorchestia platensis*. *Platorchestia platensis* can acclimate to a secondary ecotope: driftwood (Wildish and Robinson 2016) which forces a change in diet with profound effects on morphology, growth, physiology and reproduction (Wildish and Robinson 2018). Such changes can lead to false conclusions during taxonomic decision-making which is solely based on morphological characters. This can result in errors of nomenclature, as occurred during a description of a new genus and species, which was ultimately recognised to be a driftwood morphotype of *O. mediterranea* (Wildish 2014, 2018). Morphological plasticity needs to be accounted for during taxonomic decision-making, as there is growing evidence that morphological plasticity is a general property of wrack generalist talitrids. The driftwood morphotype of *O. mediterranea* also experienced a reduced growth pattern as in driftwood-acclimated *P. platensis*. This could also be the case for *O. gammarellus* which was found in driftwood, as a concomitant of the xylophagous specialist, *Macarorchestia roffensis* (Wildish, 1969) and described then as juveniles (Wildish 1982). Perhaps the juveniles were actually driftwood morphotypes of *O. gammarellus*? We believe this is worth following up experimentally (Suggestion #1).

Evolutionary ecology

Apart from the three amphi-Atlantic talitrids, inclusive of *O. gammarellus*, the talitrid biodiversity of the east and west coasts of the North Atlantic Ocean lack species in common (table 1 in Wildish and Chang (2017)). Thus, for the sand-burrowing ecotype there are five species (in one genus) in the northwest and six species (in five different genera) in the north-eastern Atlantic. For the wrack generalist ecotype, there are five species in the northwest versus five (four if *montagui* is re-assigned to new genus, see above) in the northeast Atlantic which all belong to the genus *Orchestia*. Palustral specialists appear to be limited to the northwest Atlantic, with three species identified morphologically, although genetic methods suggest up to an additional seven species or subspecies (Radulovici

2012). Driftwood specialists appear to be limited to the northeast Atlantic with five species in a single genus.

Apart from the three amphi-Atlantic species, the different talitrid fauna on both coasts we consider as evidence that long-term separation occurred after isolation of the two coasts by continental drift in the upper Cretacious/Eocene (Bousfield 1984). The single species of *Orchestia* on the northwest Atlantic coast (versus five, or four, *Orchestia* species on the northeast Atlantic coast) does not support a 'proto-*gammarellus*' presence in the Eocene here either. We would expect more *Orchestia* species diversity, in line with that of the northeast Atlantic *Orchestia*, if 'proto-*gammarellus*' had been present since the Eocene.

In post-glacial times, colonising *O. gammarellus* in Iceland would reach an open supralittoral wrack habitat, without competitors, whereas in Newfoundland and Maritime Canada, they would compete with *P. platensis*, which was spreading northwards following glacial retreat. Competition between these two species (Persson 2001) is the likely explanation for the sporadic distribution of *O. gammarellus* and its replacement by *P. platensis* at several isolated beaches during the last 50 years (Wildish, unpublished data).

Dispersal ecology

Sceptics of dispersal have condemned it as immeasurable and unimportant, but evidence of a resurgence of interest in natural dispersal was identified by Nathan (2001). Both Henzler and Ingólfsson (2008) and Myers and Lowry (2020) appear to be sceptics of natural dispersal in *O. gammarellus*. Ingólfsson (1995, 2006) conducted intensive studies of floating wrack off the coast of Iceland without finding *O. gammarellus* within it. Yet, cursory studies (five sampling excursions) in the Medway Estuary, England (Wildish 1970) found one adult individual of *O. gammarellus* in floating wrack in one sample on one sampling excursion. Clearly, the Estuary is the right place to seek evidence of passive dispersal and more intensive studies are needed in estuaries (Suggestion #2). Convincing evidence of passive dispersal at sea was provided by studying the stomach contents in several species of inshore fish which contained supralittoral talitrids (species undetermined, but likely to be *O. gammarellus*) off the Scottish coast (Gibson and Robb 1996) and in a macrotidal saltwater marsh inlet in France (Laffaille et al. 1999) where the prey was predominantly *O. gammarellus*. These findings show that the talitrids were predated by fish whilst they were present in the sea.

The range of *O. gammarellus*, from the north-eastern Atlantic Islands (Azores, Madeira, Canaries) to the Lofoten Islands, demonstrates that this species has dispersed widely within the North Atlantic. In a largely theoretical study of dispersal, Wildish (2012) proposed a lineal 'island' theory to account for the passive dispersal in floating wrack or floating driftwood. An important implication for all wrack generalist ecotypes with the ability to acclimate to a woody diet is that, when they do so in natural conditions, they may become subjects of long-range dispersal in floating driftwood. The theory helped to determine the dispersal potential of the three amphi-Atlantic talitrids (inclusive of *O. gammarellus*) with the user-friendly predictive model of present-day surface currents in the North Atlantic (van Sebille 2014). Four starting points for dispersal on the northeast Atlantic coast (Lands End, England to the Canary Islands) were modelled (Wildish and Chang 2017) and the results show that *O. gammarellus* could not be passively dispersed in either wrack or driftwood in the east to west direction. For the reverse direction, from west to east, a talitrid capable of living within driftwood could survive long enough to make the trip as a passenger within a driftwood raft, because of the fast Gulf Stream currents streaming in the direction of Europe. Unfortunately, we did not model starting points in Scotland or from the Norwegian Atlantic coasts and so are unable to determine if passive dispersal from there to Iceland was feasible given contemporary oceanographic conditions. The Norwegian current (Anon 1979) flows in a north-easterly direction close to the Atlantic Norwegian coast carrying potential dispersers in a counter-clockwise current around the Norwegian Sea and eventually to Iceland.

Within the last ten thousand years, during which humans have travelled to most parts of the planet and established trading routes by marine transport, they have often taken with them hitchhikers which colonise the new habitats. This process of synanthropy has been identified amongst talitrids, particularly those of terrestrial origin which come in soil or attached to imported tropical plants (e.g. Shoemaker (1935); Gregory (2016)). Henzler and Ingólfsson (2008) mentioned occasional accidental transport of *O. gammarellus* by ships associated with rocks, sand or other nearshore debris. An obvious candidate for transport would be in the wooden ships used to transport the Vikings from Norway to Iceland beginning in 874 AD and to Greenland in 982 (Anon 2022). The ships traversing the northern Atlantic used by the colonisers were stout 'knorr' or cargo ships, some 16–22 m in length and broad in beam and capable of carrying up to 25 tonnes of cargo, including live horses and cattle (Anon 2022). It is not clear whether they used ballast (stones, gravel or sand) in the keel, but if so, it would have been obtained by beaching the boat and loading directly from the beach, with the possibility that wrack and talitrids would have been inadvertently included.

The alternative mechanism of natural dispersal considered by Henzler and Ingólfsson (2008) to Iceland involved floating wrack (= floating seaweed). However, extensive field studies examining contemporary samples of this material showed that *O. gammarellus* was not present in coastal seas off Iceland (Ingólfsson 2006). This caused Henzler and Ingólfsson (2008) to discard natural dispersal in favour of synanthropic dispersal to Iceland.

Molecular genetics

Genetically separate lineages of multicellular organisms accumulate increasing amounts of DNA sequences which diverge during the passage of time. As a result, it is possible to estimate the geological time at which divergence first occurred using DNA sequence data. The mitochondrial cytochrome oxidase I (COI) gene is widely used for species identification and can also be used to estimate divergence times of two genetically separate lineages. Loeza-Quintana et al. (2019) used COI data from multiple pairs of arthropod species and estimated the rate of divergence at 5 to 5.2% per million years (Kimura 2-parameter corrected distance); they review earlier studies with estimates for arthropods ranging from 1.4 to 6.6% per million years.

Henzler and Ingólfsson (2008) sequenced a 532-bp fragment of COI in *O. gammarellus* from north-western Europe, Iceland and Canada. All three hypotheses for the origin of *O. gammarellus* (synanthropic dispersal, post-glacial natural dispersal and Eocene vicariance) make different predictions about the amount of DNA divergence to be expected. Considering an estimate of 5% divergence per million years, if the Icelandic/Canadian populations of *O. gammarellus* were completely isolated since the first Viking ships sailed to Iceland ~ 1100 years ago, the expected divergence would be only 0.007%, which would likely be undetectable with a 532-bp fragment. Postglacial dispersal 20,000 years ago would produce an estimated divergence of 0.1% or one site changed in 1000, so the 532-bp COI fragment might have some haplotypes that were found in Canada or Iceland, but were not present in Europe. However, if Canadian and Icelandic populations of *O. gammarellus* had been genetically isolated since the Eocene, their COI sequences would be saturated with divergence at every site that was not constrained by selection.

Henzler and Ingólfsson (2008) found a single, major haplotype in most of their European and Icelandic samples, which was also present in a minority of Canadian *O. gammarellus*. All of the other haplotypes in their sample differed from the most common one by at most two nucleotides. This is inconsistent with the genetic separation of north-eastern and north-western Atlantic populations of *O. gammarellus* since the Eocene. Henzler and Ingólfsson (2008) also estimated the divergence time between Icelandic/Canadian versus European populations to be about 14,000 to 18,000 years, which fits better with the post-glacial natural dispersal hypothesis rather than with synanthropic Viking colonisation, which occurred at the earliest 1,148 years BP.

Henzler and Ingólfsson (2008) showed that Iceland had a common minority haplotype that was not found in their European or Canadian samples and the most common haplotype in Canada was not found in any other sample. The presence of a few local haplotypes is consistent with an early postglacial dispersal. However, Henzler and Ingólfsson (2008) also found considerable divergence, including some local haplotypes, amongst sampling sites within Europe. One other possible way of explaining this result is that the Icelandic/Canadian populations originated by recent synanthropic dispersal from a source population that Henzler and Ingólfsson (2008) did not sample.

Myers and Lowry (2020) described *O. gammarellus* populations in Iceland and Atlantic Canada as a new species, *O. forchuensis*, based solely on morphological differences and did not provide an adequate discussion of the COI sequence data of Henzler and Ingólfsson (2008).

Other published molecular data of pairs of closely related species generally differ in their COI sequences by several percent; Hebert et al. (2003) found that 99.9% of pairs of congeneric crustacean species differed by 1–20%. Costa et al. (2009) considered 16 species of *Gammarus* and found that the closest pair of species, *G. insensibilis* and *G. aequicauda*, differed by 5.2%. The closest pair of *Orchestia* species in Pavesi et al. (2015), *O. mediterranea* and *O. aestuarensis* differed by 11%. Davalos et al. (2018) sequenced COI and histone H3 in European populations of *O. gammarellus*, *O. montagui*, *O. stephenseni*, *O. mediterranea* and *O. aestuarensis*; the most similar pair of species, *O. mediterranea* and *O. aestuarensis*, differed by over 5%. The reason that the Kimura 2-parameter corrected distance was different in the latter species pair was that Pavesi et al. used a longer fragment of COI (497 bp) than Davalos et al. (363 bp) and because the distances in the latter combine COI data with the more conservative histone H3 gene.

We used MEGA version 11 (Tamura et al. 2021) and the COI data of Henzler and Ingólfsson (2008) to calculate the average Kimura 2-parameter corrected distance between "*O. forchuensis*" (Canada plus Iceland) and *O. gammarellus* from Europe. The distance was only 0.1%, with many individuals in the two groups sharing identical haplotypes. This is much less than the distances between closely-related pairs of well-established other *Orchestia* species. The COI data are, therefore, in conflict if the Icelandic/Canadian populations are considered as a separate species.

Molecular genetic methods applied to amphipod taxonomy are an important addition to morphology, rather than a replacement of it, resulting in a more accurate and useful combined discipline. The particular molecular genetic methods needed to achieve this include:

- Determining genetic distances between populations of closely-related species.
- Determining the geological age of separation between isolated populations of the same or closely-related species.
- Providing a convergence-free talitrid phylogeny which is central to an accurate phylogenetic tree, as the proper basis for defining the higher levels of taxonomy within Talitroidea.

The COI phylogeny of Henzler and Ingólfsson (2008) suggested a population expansion from a single, bottlenecked source population which arrived in Iceland at some point during the last post-glacial period.

Conclusions

Since the dispersal and zoogeographic distribution of *Orchestia* in the North Atlantic is hypothesised to occur either in the recent post-glacial or distant (Eocene/Cretaceous) past, direct evidence to determine how it happened is impossible to obtain. Consequently, the best approach to this question is to use an accumulation of indirect, circumstantial evidence inclusive of molecular genetic methods, to determine which hypothesis is more likely to be the correct one. The circumstantial evidence, so far available, favours post-glacial natural dispersal. In summary the arguments for this point of view are as follows:

- Talitrid species diversity differences on the west and east coasts of the North Atlantic are consistent with a split and isolation due to continental drift in the Eocene. A single species of *Orchestia* on the west coast (versus 5 or 4, on the east coast) is not consistent with similar speciation rates on the east coast since an Eocene split.
- *Orchestia gammarellus* on the northwest Atlantic coast is only present in areas affected by glacial ice during the last Ice Age and no refuges of this species are known south of the ice limit at Cape Cod.
- The COI genetic data of Henzler and Ingólfsson (2008) indicate that the genetic distance between populations of Canadian/Icelandic versus European *O. gammarellus* are very small and all haplotypes are within two base pairs of a common haplotype.
- The COI genetic data of Henzler and Ingólfsson (2008) estimated the divergence times between Canadian/Icelandic versus European *O. gammarellus* populations to be consistent with post-glacial, rather than of Eocene age.

Given that post-glacial natural dispersal of *O. gammarellus* in the North Atlantic is the more plausible one, we question the validity of a new species name: *O. forchuensis* Myers & Lowry, 2020, proposed for the Canadian/Icelandic specimens. Paraphrasing Myers (1997): current amphipod taxonomy is based solely on morphological characters (with no consideration of reproductive capabilities or genetic data) and the subjective conclusion of the taxonomist as to what constitutes a species. The minor morphological differences between the proposed two taxa and compelling genetic evidence of Henzler and Ingólfsson (2008) suggests that populations on both sides of the North Atlantic belong to one species. We propose that an experimental cross-breeding test (Suggestion #3) would help to decide whether one or two species were involved.

Suggestions for further studies

1. Experimental investigation to determine if *O. gammarellus* can be acclimated to live in and feed on wet decomposing driftwood. A positive finding here would qualify *O. gammarellus* as a potential long-distance disperser in driftwood.
2. Undertake many field excursions in North Atlantic estuaries where *O. gammarellus* is common, to identify the macrofauna in floating wrack and driftwood. Sampling excursions would be triggered by storm events whenever they occur during the year and not just during the summer. Driftwood should be broken up sufficiently in order to search for *O. gammarellus* deep in crevices and burrows. Further direct evidence would bolster (or deny) the general case for passive, natural dispersal in floating wrack/driftwood by *O. gammarellus*.
3. Experimental cross breeding between individuals of *O. gammarellus* from Canada/Iceland with individuals from European shores. Successful matings would support either of the two post-glacial hypotheses. Unfortunately, unsuccessful matings would support either the origin of a more recent genetic isolation mechanism or Eocene divergence of *O. gammarellus*.
4. An in-depth geographic survey of COI variation in *O. gammarellus* from Europe. Henzler and Ingólfsson (2008) sampled one location in Ireland, Scotland, England and Sweden and two locations in southern Norway. This is a small subset of the European home range of *O. gammarellus*. A more thorough survey of COI variation with additional genetic markers, including rapidly evolving nuclear sequences, from the entire range of *O. gammarellus* in the eastern Atlantic might distinguish between post-glacial natural dispersal and historic anthropogenic dispersal. If trans-Atlantic dispersal occurred synanthropically, the local haplotypes found in Iceland and Canada should also be found on European beaches. If common haplotypes are present only in Iceland and Canada, it would suggest that new mutations had occurred since dispersal and persisted for long enough to estimate their divergence times.

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References

Anon (1979) World Atlas. Montreal, Geografic International.

Anon (2022) History of Iceland/History of Greenland/Viking ships. https://en.wikipedia.org/wiki/History_of_Iceland/History_of_Greenland/Viking_ships [Accessed 23/03/2022]

Bellan-Santini D, Ruffo S (2003) Biogeography of benthic marine Amphipods in Mediterranean Sea. Biogeographia 24: 273–292. https://doi.org/10.21426/B6110176

Bousefield EL (1973) Shallow-water gammaridean Amphipoda of New England. Cornell University Press, Ithaca and London, 312 pp.

Bousfield EL (1984) Recent advances in the systematics and biogeography of landhoppers (Amphipoda; Talitridae) of the Indo-Pacfic region. In: Radovsky FJ, Raven PH, Sohmer SH (Eds) Biogeography of the Tropical Pacific. Bishop Museum Special Publication 72: 171–210.

Buckland PC, Perry DW, Gislason GM, Dugmore AJ (1986) The pre-Landnam fauna of Iceland: A palaeontological contribution. Boreas 15(2): 173–184. https://doi.org/10.1111/j.1502-3885.1986.tb00081.x

Costa FO, Henzler CM, Lunt DH, Whiteley NM, Rock J (2009) Probing marine *Gammarus* (Amphipoda) taxonomy with DNA barcodes. Systematics and Biodiversity 7(4): 365–379. https://doi.org/10.1017/S1477200009990120

Dahl E (1967) Land amphipods from the Azores and Madeira. Boletim do Musen Municipal do Frenchal 21: 8–23.

Davalos D, De Metthaeis E, Latella L, Tarocco M, Özbek M, Vonk R (2018) On the molecular and morphological evolution of continental and insular *Cryptorchestia* species, with an additional description of *C. garbinii* (Talitridae). ZooKeys 783: 37–54. https://doi.org/10.3897/zookeys.783.26179

Gibson RN, Robb L (1996) Piscine predation on juvenile fishes on a Scottish sandy beach. Journal of Fish Biology 49(1): 120–138. https://doi.org/10.1111/j.1095-8649.1996.tb00009.x

Gregory SJ (2016) On the terrestrial landhopper *Arcitalitrus dorrieni* (Hunt, 1925) (Amphipoda: Talitridae): identification and current distribution. Bulletin of the British Myriapod and Isopod Group 29: 1–11.

Hebert PDN, Ratnasingham S, de Waard JR (2003) Barcoding animal life: Cytochrome c oxidase subunit 1 divergences among closely related species. Proceedings of the Royal Society of London: Series B, Containing Papers of a Biological Character 270(Supp l.): s96–s99. https://doi.org/10.1098/rsbl.2003.0025

Henzler CM, Ingólfsson A (2008) The biogeography of the beach-flea, *Orchestia gammarellus* (Crustacea, Amphipoda, Talitridae) in the North Atlantic with special reference to Iceland: A morphometric and genetic study. Zoologica Scripta 37: 57–70. https://doi.org/10.1111/j.1463-6409.2007.00307.x

Ingólfsson A (1973) *Orchestia gammarellus* (Pallas) (Amphipoda: Talitridae) recorded from Iceland. Náttúrufræðingurinn 43: 170–174. [In Icelandic]

Ingólfsson A (1995) Floating clumps of seaweed around Iceland: Natural microcosms and means of dispersal for some fauna. Marine Biology Berlin 150: 1333–1343. https://doi.org/10.1007/s00227-006-0457-3

Ingólfsson A (2006) The intertidal seashore of Iceland and its animal communities. Zoology of Iceland I(7): 1–85.

Kellogg TB (1980) Paleoclimatology and paleo-oceanography of the Norwegian and Greenland seas: glacial-interglacial contrasts. Boreas 9: 115–137. https://doi.org/10.1111/j.1502-3885.1980.tb01033.x

Laffaille P, Feunten E, Lefeure J-C (1999) Competition alimentaire entre deux especes de gobies *Pomatoschisius lozanoi* (de Buen) et *P. minutus* (Pallas), dans un marais sale macrotidal. Comptes Rendus de l'Académie des Sciences. Série III, Sciences de la Vie 322: 123–135. https://doi.org/10.1016/S0764-4469(00)86656-1

Loeza-Quintana T, Carr CM, Khan T, Bhatt YA, Lyon SP, Hebert PDN, Adamowicz SJ (2019) Recalibrating the molecular clock for Arctic marine invertebrates based on DNA barcodes. Genome 62(3): 200–216. https://doi.org/10.1139/gen-2018-0107

Myers AA (1997) Biogeographic barriers and the development of marine biodiversity. Estuarine, Coastal and Shelf Science 44(2): 241–248. https://doi.org/10.1006/ecss.1996.0216

Myers AA, Lowry JK (2020) A revision of the genus *Orchestia* Leach, 1814 with the reinstatement of *O. inaequalipes* (K. H. Barnard, 1951), the designation of a neotype for *Orchestia gammarellus* (Pallas, 1776) and the description of three new species (Crustacea: Amphipoda: Talitridae: Talitrinae). Zootaxa 4808(2): 201–250. https://doi.org/10.11646/zootaxa.4808.2.1

Nathan R (2001) The challenges of studying dispersal. Trends in Ecology & Evolution 16(9): 481–483. https://doi.org/10.1016/S0169-5347(01)02272-8

Pavesi L, Wildish DJ, Gasson P, Lowe M, Ketmaier V (2015) Further morphological and molecular studies of driftwood hoppers (Crustacea: Amphipoda: Talitridae) from Mediterranean/north-east Atlantic coastlines. Journal of Natural History 49(17–18): 1047–1071. https://doi.org/10.1080/00222933.2014.974708

Persson LE (1999) Growth and reproduction in two brackish-water populations of *Orchestia gammarellus* (Amphipoda, Talitridae) in the Baltic Sea. Journal of Crustacean Biology 19(1): 53–59. https://doi.org/10.2307/1549546

Persson L-E (2001) Dispersal of *Platorchestia platensis* (Krøyer) (Amphipoda: Talitridae) along Swedish coasts: a slow but successful process. Estuarine, Coastal and Shelf Science 52(2): 201–210. https://doi.org/10.1006/ecss.2000.0735

Radulovici AE (2012) A tale of two biodiversity levels from DNA barcoding of selected North Atlantic crustaceans. Ph. D. thesis, University of Quebec, Rimouski, 245 pp.

Sæmundsson B (1937) Icelandic Malacostraca in the Museum of Reykjavik. Vísindaféjlag Islendinga 20: 1–32.

Shoemaker CR (1935) The occurrence of the terrestrial amphipods *Talitrus alluaudi* and *Talitrus sylvaticus* in the United States. Journal of the Washington Academy of Sciences Ser. 26: 60–64.

Stephensen K (1940) The Amphipoda of N. Norway and Spitsbergen with adjacent waters. Tromsø Museums skrifter 3: 279–362.

Tamura K, Stecher G, Kumar S (2021) MEGA11: Molecular Evolutionary Genetics Analysis version 11. Molecular Biology and Evolution 38(7): 3022–3027. https://doi.org/10.1093/molbev/msab120

Van Sebille E (2014) Adrift.Org.au – a free, quick and easy tool to quantitatively study surface drift in the global ocean. Journal of Experimental Marine Biology and Ecology 461: 317–322. https://doi.org/10.1016/j.jembe.2014.09.002

Wildish DJ (1970) Some factors affecting the distribution of *Orchestia* Leach in estuaries. Journal of Experimental Marine Biology and Ecology 5(3): 276–284. https://doi.org/10.1016/0022-0981(70)90007-9

Wildish DJ (1982) Talitroidea (Crustacea, Amphipoda) and the driftwood ecological niche. Canadian Journal of Zoology 60(12): 3071–3074. https://doi.org/10.1139/z82-390

Wildish DJ (2012) Long distance dispersal and evolution of talitrids (Crustacea: Amphipoda: Talitridae) in the northeast Atlantic islands. Journal of Natural History 46(37–38): 2329–2348. https://doi.org/10.1080/00222933.2012.708458

Wildish DJ (2014) New genus and two new species of driftwood hoppers (Crustacea, Amphipoda, Talitridae) from northeast Atlantic and Mediterranean coastal regions. Zoosystematics and Evolution 90(2): 133–146. https://doi.org/10.3897/zse.90.8410

Wildish DJ (2018) *Neotenorchestia* Wildish, 2014 is a junior synonym of *Orchestia* Leach, 1814. Zoosystematics and Evolution 94(2): 545–546. https://doi.org/10.3897/zse.94.28876

Wildish DJ, Chang BD (2017) Is dispersal of talitrids (Amphipoda) in the North Atlantic feasible? Crustaceana 90(2): 207–224. https://doi.org/10.1163/15685403-00003636

Wildish DJ, Robinson SMC (2016) A new secondary ecotope for talitrids: Driftwood in the Bay of Fundy. Crustaceana 89(6–7): 737–757. https://doi.org/10.1163/15685403-00003557

Wildish DJ, Robinson SMC (2018) Effect of diet on oxygen uptake rate in the talitrid amphipod, *Platorchestia platensis*. Marine and Freshwater Behaviour and Physiology 51(5): 293–299. https://doi.org/10.1080/10236244.2019.1567267